BENTHIC COMMUNITY STRUCTURE IN TWO ADJACENT STREAMS IN YELLOWSTONE NATIONAL PARK FIVE YEARS AFTER THE 1988 WILDFIRES

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ABSTRACT.—Physical characteristics, benthic macroinvertebrates, and periphyton assemblages in two adjacent head-water streams in Yellowstone National Park were evaluated five years after the 1988 wildfires. The catchment of one stream was burned by wildfire (burned stream) while the other catchment was unburned (unburned stream). Physical measures revealed channel alteration in the burned stream relative to the unburned stream. Periphyton biomass was lower in the burned than the unburned stream (29.2 vs. 50.5 g/m^2 AFDM, respectively), further demonstrating the unstable physical conditions of that system. Kendall's coefficient of concordance (an index of similarity) between diatom assemblages was 0.22, indicating distinct assemblage composition between streams. *Navicula permitis* Hust. was the most abundant diatom in the burned stream while *Hannaea arcus* (Ehr.) Patr. was dominant in the unburned stream. Macroinvertebrate taxa richness, density, and biomass were all greater in the unburned stream, although Chironomidae was the most abundant taxon in both streams. Results suggest the removal of terrestrial/riparian vegetation by wildfire can directly influence stream benthic assemblages by altering the inherent disturbance regime of the physical habitat templet.

Key words: wildfire, streams, disturbance, macroinvertebrates, diatoms, benthic habitat, Yellowstone National Park.

Physical disturbance, acting at various spatial and temporal scales, often is the predominant factor structuring stream benthic communities (Minshall 1988, Resh et al. 1988). Further, physical disturbances may be viewed in a hierarchical framework, with the effects of small-scale disturbances altered (intensified or mediated) by large-scale disturbance events (sensu O'Neill et al. 1986). Wildfire, as a large-scale disturbance, directly influences stream biotic structure and function by affecting the physical habitat of stream ecosystems (Minshall et al. 1989, Minshall and Brock 1991, Richards and Minshall 1992, Robinson et al. 1994, Mihuc et al. in press, Robinson and Minshall in press). In lotic ecosystems, physical disturbance also may constrain the establishment of biotic controls, such as competition and predation, on benthic community structure (McAuliffe 1984, Minshall and Petersen 1985, Resh et al. 1988).

Wildfire burned extensive portions of the Greater Yellowstone Ecosystem during the summer of 1988. Over 32% of the streams in Yellowstone National Park (YNP) were affected to varying degrees by wildfires (Minshall et al. 1989, Minshall and Brock 1991, Robinson et al.

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biomass determination, expressed as grams ash-free dry mass (AFDM) per m^2. The material was dried at 50°C for 24 h, weighed on a Sauter balance (Model AR 1014), ashed at 550°C for a minimum of 3 h, rehydrated, redried at 50°C, then cooled to ambient temperature in a desiccator and reweighed. The difference in weights equaled the AFDM of the sample.

Diatom samples were collected in each stream, after Robinson and Rushforth (1987), from three to five rock substrata representing the predominant habitat type (typically riffles). Samples were composited, preserved with 5% formalin, and returned to the laboratory. The composite sample was boiled in concentrated nitric acid, rinsed, mounted in Naphrax mountant, and examined under 1000X oil immersion using a Zeis RA microscope with Nomarski optics (St. Clair and Rushforth 1976). Relative abundances of diatom taxa were determined by counting a minimum of 1000 diatom valves from each stream. Diatoms were analyzed in terms of species richness, Simpson's index, and Kendall's coefficient of concordance (an index of similarity using all taxa with a relative abundance >1%). Other algal groups such as Chlorophyta (green algae) and Cyanobacteria (blue-green algae) were not abundant at the time of sampling and thus were not considered in the present study.

One benthic sample was collected from a riffle/run habitat (pools were rare and not sampled) near each transect and analyzed for macroinvertebrates and benthic organic matter (BOM). Samples were collected using a Surber sampler (250 μm mesh), preserved with 5% formalin, and returned to the laboratory. Woody debris >5 cm in length that was collected in the benthic samples was rinsed of invertebrates and removed from the samples. In the laboratory, macroinvertebrates were hand-sorted from the benthic detritus with the aid of a 3X dissecting microscope, identified to the lowest feasible level (usually genus), enumerated, dried at 50°C for a minimum of 48 h, then cooled to ambient temperature in a desiccator and weighed. Dry weights, in milligrams, were determined on a Cahn (Model 25) electrobalance. The benthic detritus from each sample was used for BOM determination. The quantity of BOM, expressed as g AFDM/ m^2, was determined as described above for periphyton. Macroinvertebrates were analyzed

in terms of density (no./m^2), biomass (mg/m^2), taxa richness, Simpson's index, and relative abundances.

Chi-squared analysis was used to test for statistical differences in median substratum size between the two streams (Zar 1984). Independent sample t tests were used to compare the other characteristics for differences between the two streams. Prior to the t-test analysis all data were log (x + 1) transformed, except substratum embeddedness and the relative abundance of invertebrate taxa (both percentage measures), which were arcsine (square root [x]) transformed (Zar 1984). Tabular results are presented as untransformed means and standard deviations. All statistical analyses were performed on SYSTAT (Wilkinson 1990).

RESULTS

Baseflow discharge was equal in the two streams (0.2 m^3/s), reflecting the similar catchment size of the burned (22 km^2) and unburned (26 km^2) streams. Mean baseflow width, near-bed water velocity, and BOM were not significantly different between the two streams ($P > .05$). Substratum embeddedness was significantly greater in the burned stream ($P = .01$), although the difference between mean values was not large (burned = 62.9, unburned = 52.8). It is not known whether this statistical difference was biologically meaningful or simply a reflection of the large sample size ($n = 100$).

Water depth at baseflow ($P < .01$) was lower and stream width at bankfull discharge greater ($P = .03$) in the burned stream than the unburned stream. Although not statistically significant ($P = .06$), the ratio of stream width: depth was greater in the burned than the unburned stream (216 and 91, respectively). The general appearance of the two streams was distinctly different (Fig. 1; Minshall personal observation). Large, woody debris and streamside riparian vegetation, which provide bank and channel stability, were noticeably absent in the burned stream.

Mean substratum size was not significantly different between the two streams ($P > .05$) in 1993, possibly because large boulders were not recorded in the measurements (see Fig. 1). We collected additional data on substratum size in August 1994 and included large boulders in the measurements. Further, substrata within

Fig. 1. Representative photographs of the burned (upper) and unburned (lower) streams five years after the 1988 wildfire. Note absence of large, woody debris and streamside riparian vegetation in the burned stream.

the bankfull channel were measured in 1994, in contrast to measures being recorded only within the baseflow channel in 1993. The 1994 results showed that mean substratum size was significantly larger in the unburned than in the burned stream ($P < .01$).

A comparison of median substratum size showed similar results to that of mean substratum size. Median substratum size was not different between the two streams when measurements excluded large boulders and were confined to the baseflow channel ($P > .05$). However, when measurements included large boulders and encompassed the bankfull channel, the difference in median size was significant ($P < .01$). Whether large boulders were present in the burned stream prior to the wildfire has yet to be determined. However, in other streams influenced by intensive wildfire, large boulders were observed to be buried by inorganic debris (primarily gravel and fine sediments) within five years following wildfire (Minshall personal observation).

The burned stream contained less periphyton chlorophyll a ($P = .06$) and AFDM ($P < .01$) than did the unburned stream (Table 1). Diatom species richness was greater in the burned (34 taxa) than in the unburned stream (27 taxa; Table 2). Simpson's index was lower for the burned than unburned stream (0.12 and 0.42, respectively). Kendall's coefficient of concordance for the two diatom communities was 0.22, suggesting distinct assemblage composition among sites. For example, *Navicula permitis* Hust. was the most abundant species in the burned stream, constituting 24.7% of

the assemblage, while *Hannaea arcus* (Ehr.) Patr. comprised 63.1% of the assemblage in the unburned stream (Table 2).

Mean macroinvertebrate density and biomass were lower in the burned than unburned stream (Table 3), but the differences were not significant ($P > .05$). For example, mean density in the burned stream was 9960 individuals/m^2, while the unburned stream had 16,950 individuals/m^2, and mean biomass (dry weight) was 1960 and 3200 mg/m^2 in the burned and unburned streams, respectively. Taxa richness and Simpson's index both were reduced in the burned stream, although the difference was significant only for Simpson's index ($P = .04$) (Table 3). The burned stream contained a mean of 15 taxa per benthic sample compared to a mean of 20 taxa for the unburned stream. The mean Simpson's index was 0.57 for the burned stream and 0.73 for the unburned stream. Chironomidae was the most abundant taxon in both streams (Table 4), although their relative abundance was significantly greater ($P = .03$) in the unburned stream. There were no statistical differences ($P > .05$) in relative abundances of other taxa common to both streams (Hydracarina, Simuliidae, *Baetis bicaudatus*, *Cinygmula*, and *Zapada columbiana*).

DISCUSSION

Alterations of the surrounding terrestrial landscape by major unpredictable disturbances such as hurricanes, volcanic eruptions, or wildfire directly influence streams draining the

TABLE 1. Means (SD) and P values for physical characteristics measured in the study streams.

	Burned		Unburned		P value
Baseflow width (m)	5.9	(2.6)	4.5	(1.8)	.46
Near-bed velocity (cm/s)	10.3	(0.1)	10.7	(0.1)	.71
BOM (g/m^2)	1.5	(0.8)	2.5	(1.2)	.20
Embeddedness (%)	62.9	(28.5)	52.8	(30.0)	.01
Baseflow depth (cm)	16.9	(11.0)	24.3	(12.5)	<.01
Bankfull width (m)	35.0	(11.9)	16.6	(1.4)	.03
Bankfull width:depth ratio	216	(101)	91	(21)	.06
Periphyton chl a (mg/m^2)	8.9	(5.5)	32.1	(19.5)	.06
Periphyton AFDM (g/m^2)	29.2	(3.7)	50.5	(9.3)	<.01
[*]Mean substratum size (cm)	14.4	(10.5)	15.0	(14.2)	.26
[**]Mean substratum size (cm)	15.5	(15.5)	27.6	(27.4)	<.01
[*]Median substratum size (cm)	12.0		11.0		.72
[**]Median substratum size (cm)	11.0		17.0		<.01

[*]Baseflow channel, large boulders excluded.
[**]Bankfull channel, large boulders included.

TABLE 2. Community measures and relative abundances (%) for the diatom assemblage of each study stream.

	Burned	Unburned
Species richness	34	27
Simpson's index (C)	0.12	0.42
Navicula pernitis Hust.	24.7	5.1
Nitzschia dissipata (Kuetz.) Grun.	17.3	4.2
Achnanthes lanceolata (Breb.) Grun.	9.8	1.7
Nitzschia paleacea Grun.	7.6	3.1
Navicula arvensis Hust.	4.8	2.4
Hannaea arcus (Ehr.) Patr.	2.1	63.1

TABLE 3. Means (SD) and P values of macroinvertebrate community measures for the study streams.

	Burned	Unburned	P value
Density (no./m²)	9963 (4730)	16,948 (8998)	.31
Biomass (mg/m²)	1956 (1056)	3198 (1274)	.19
Taxa richness	15.0 (3.7)	20.4 (2.6)	.58
Simpson's index (C)	0.57 (0.09)	0.73 (0.10)	.04

affected watersheds. For example, the Mt. St. Helens eruption of 1980 dramatically changed drainage patterns and river networks, eliminated terrestrial vegetation, and caused major debris flows that scoured stream channels (Wilzbach et al. 1983, Hawkins 1988). However, high spatial variation in the intensity of these major disturbances may occur, causing temporal differences in recovery patterns (Yount and Niemi 1990). In catchments of YNP the relative area burned ranged from <10% to >90% (Minshall and Brock 1991). Further, the degree of alteration of stream habitat was highly correlated with percent of catchment burned (Robinson and Minshall in press).

In the present study significant differences were observed in the benthic habitat of the two streams. The width:depth ratio of the burned stream was greater than that of the unburned stream. Anderson (1992) also observed increased width:depth ratios following major disturbances in streams of the Cascade Mountains. With large boulders included in the measurements, the unburned stream exhibited significantly greater substratum size. Gurtz and Wallace (1984) demonstrated that large substrata could mediate the effects of large-scale disturbances by providing stable habitat for benthic organisms. At the time of sampling, the burned stream did not contain the larger-sized substrata found in the unburned stream. It is probable that the larger substrata in the burned stream were buried by inorganic sediments following the wildfire, as has been observed in other YNP streams (Minshall personal observation). Thus, one effect of the wildfire appeared to be alteration of the substrata in such a manner as to make the benthic habitat more susceptible to future disturbances (e.g., Gurtz and Wallace 1984).

Lamberti et al. (1991) found that faunal densities and macroinvertebrate species richness had recovered within one year following a major debris flow in an Oregon stream. In central Idaho, however, streams disturbed by wildfire and unburned reference streams showed little similarity in macroinvertebrate assemblages, even after five years of recovery (Richards and Minshall 1992). Similarly, in the present study the influence of wildfire was still apparent after five years. Macroinvertebrate community structure was not similar between the two systems, despite their close proximity to each other (0.5 km). Most researchers agree that recovery of the benthic community will correspond to recovery of the surrounding landscape (Steinman and Lamberti 1988, Minshall et al. 1989, Lamberti et al. 1991, Minshall and Brock 1991, Anderson 1992, Richards and Minshall 1992, but see Hawkins 1988).

Primary producers (lotic algae) may recover sooner than consumers (macroinvertebrates and fish) because of their much shorter life cycles, and subsequently they may influence recovery of the higher trophic levels (Steinman and McIntire 1990). In the present study, periphyton biomass (as AFDM) in the unburned stream was 1.7X greater than in the burned stream, implying a present lack of recovery by primary producers in the burned system. Macroinvertebrate taxa richness also was greater in the unburned stream than in the burned stream. How functional or structural recovery of macroinvertebrates is related to algal recovery following wildfire has yet to be determined, but provides an interesting and important avenue for future research. Algae have shorter life cycles and reduced mobility relative to macroinvertebrates, and possibly the two groups respond differently to large-scale disturbances.

TABLE 4. Mean (SD) density and relative abundance of the 10 most abundant macroinvertebrate taxa from each stream. These taxa constituted >90% of the assemblage in their respective streams.

Taxa	Density (no./m²)	Relative abundance (%)
---------- Burned ----------		
Chironomidae	5437 (2218)	59.7 (19.2)
Simuliidae	2737 (4583)	18.2 (24.1)
Baetis bicaudatus	576 (346)	8.1 (6.3)
Hydracarina	148 (232)	1.5 (2.3)
Epeorus albertae	95 (123)	1.0 (1.2)
Zapada columbiana	90 (72)	1.0 (0.7)
Epeorus longimanus	80 (125)	0.5 (0.7)
Cinygmula	75 (71)	0.8 (0.7)
Rhithrogena	37 (52)	0.3 (0.3)
Ameletus cooki	22 (15)	0.3 (0.2)
---------- Unburned ----------		
Chironomidae	14,676 (8289)	84.7 (6.7)
Hydracarina	372 (253)	2.1 (1.6)
Cinygmula	314 (187)	1.7 (0.8)
Zapada columbiana	310 (215)	1.6 (0.6)
Simuliidae	307 (181)	3.8 (5.3)
Baetis bicaudatus	125 (60)	1.4 (1.7)
Drunella coloradensis	75 (64)	0.4 (0.5)
Rhyacophila angelita	73 (55)	0.4 (0.2)
Rhyacophila tucula	52 (29)	0.3 (0.1)
Kogotus	52 (35)	0.3 (0.2)

After five years of recovery, the channel of the burned stream still appeared unstable as indicated by different diatom assemblages between the two streams. For example, the small, adnate diatom *Navicula permitis* Hust. was predominant in the burned stream but was found in relatively low abundance in the unburned stream. *N. permitis* was predominant in other YNP streams influenced by the 1988 wildfires, and it has been suggested that a diatom community with an abundance of *N. permitis* is indicative of more physically disturbed stream environments (Robinson et al. 1994). Further, Robinson et al. (1994) showed diatom recovery among 14 streams in Yellowstone was inversely related to degree of disturbance by wildfire. Similarly, Steinman and Lamberti (1988) found little recovery, after six years, in the composition of algal communities in intensively disturbed streams of Mt. St. Helens. In summary, benthic community recovery patterns appeared to be related to the recovery of stream physical habitat which, five years after the 1988 wildfires, still displayed evidence of instability. When examining the recovery of benthic communities following large-scale disturbance, one must remain aware of the connections between the terrestrial landscape, lotic habitat, and benthic organisms.

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